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Offshore spawning and year-class strength of northern cod (2J3KL) during the fishing moratorium, 1994-1996.

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Abstract

An offshore acoustic survey was conducted during June 1994-1996 in the vicinity of Hawke Channel, traditionally reported as the most important offshore spawning area of northern cod (2J3KL). Estimates of spawner abundance and maturities at age combined with published estimates of fecundity at age were used to calculate the potential number of eggs spawned each year offshore. A pelagic juvenile fish survey was conducted during August-September each year, covering the shelf region offshore from Hamilton Bank to the southern Grand Banks (Divisions 2J3KLNO), including all inshore areas along the northeast coast of Newfoundland. Absolute estimates of abundance for pelagic juvenile cod, typically 60-80 days old, were used to calculate natural mortality between the egg and pelagic juvenile stages. The abundance of cod surveyed offshore in June ranged between 16 – 21 million fish among years. There was a sharp decline in the abundance of spawning cod from 1994 – 1996 contrasted with an increase the abundance of juveniles. Spawning biomass decreased from 17,500 t in 1994 to 8,200 t in 1995 to 5,500 t in 1996. The decline in mature cod resulted from the decline and disappearance of cod from the 1987-89 year-classes. This translated into a decline in the number of eggs spawned from 3.7×10^{12} eggs in 1994 to 2.7×10^{11} eggs in 1996. These declines were mirrored in the distribution and abundance of pelagic juvenile cod. In 1994, juvenile cod were distributed widely offshore and throughout the inshore area. By 1995, few juveniles were observed offshore but they were distributed abundantly throughout the inshore area. In 1996, no juveniles were sampled offshore and only small numbers of juveniles were encountered inshore. Abundance of pelagic juvenile cod declined from 3.1×10^{9} fish in 1994, to 1.5×10^{9} fish in 1995 to 1.8×10^{8} fish in 1996. Natural mortality was estimated to increase from $-0.068\ d^{-1}$ in 1994 to $-0.084\ d^{-1}$ in 1995 to $-0.112\ d^{-1}$ in 1996 for pelagic cod sampled offshore. The decline in spawning fish offshore occurred two years after the implementation of a fishing moratorium for this stock and, therefore, cannot be linked to fishing. This decline in spawning fish combined with the increased rate of natural mortality between the egg and pelagic juvenile stages among years is consistent with depensation mechanisms for a fish population.

Résumé

Un relevé acoustique hauturier a été effectué au cours des mois de juin de 1994 à 1996 dans la région de Hawke Channel, considéré depuis longtemps comme la plus importante zone de frai hauturière de la morue du Nord (2J3KL). Des estimations de l'abondance des géniteurs et de la maturité selon l'âge, combinées aux estimations publiées de la fécondité selon l'âge, ont été utilisées pour le calcul de la ponte annuelle en zone hauturière. Un relevé des poissons juvéniles pélagiques a été réalisé en août-septembre de chaque année, portant sur la zone hauturière de plateau s'étendant du banc Hamilton jusqu'au sud des Grands Bancs (divisions 2J3KLNO) et englobait toutes les zones côtières de la côte nord-est de Terre-Neuve. Des estimations de l'abondance absolue des morues juvéniles pélagiques, normalement âgées de 60 à 80 jours, ont été appliquées au calcul de la mortalité naturelle entre les stades d'œuf et de juvénile pélagique. L'abondance des morues en juin dans la zone hauturière du relevé variait de 16 à 21 millions selon l'année. On a noté un déclin net de l'abondance des géniteurs de 1994 à 1996 qui s'opposait à une augmentation de celle des juvéniles. La biomasse des géniteurs a diminué de 17 500 t en 1994 à 8 200 t en 1995 et à 5 500 t en 1996. Ce déclin des morues matures résultait de la diminution et de la disparition de morues des classes d'âge de 1987 à 1989. Cela s'est traduit par une diminution de la ponte qui est passée de $3,7 \times 10^{12}$ œufs en 1994 à $2,7 \times 10^{11}$ œufs en 1996. Ces réductions se sont reflétées dans la répartition et l'abondance des morues juvéniles pélagiques. En 1994, les juvéniles se trouvaient largement dispersés au large et dans toute la zone côtière. En 1995, très peu étaient observés en zone hauturière, mais ils étaient abondants dans toute la zone côtière. En 1996, aucun juvénile n'a été capturé au large et un nombre restreint a été décelé en zone côtière. L'abondance des morues juvéniles pélagiques a chuté de $3,1 \times 10^{9}$ poissons en 1994 à $1,5 \times 10^{9}$ poissons en 1995 et à $1,8 \times 10^{8}$ poissons en 1996. Il a été estimé que la mortalité naturelle chez les morues pélagiques prélevées en zone hauturière avait augmenté pour passer de $-0.068\ d^{-1}$ en 1994 à $-0.084\ d^{-1}$ en 1995 et à $-0.112\ d^{-1}$ en 1996. Cette baisse des géniteurs en zone hauturière s'est produite deux ans après l'imposition d'un moratoire de la pêche de ce stock et ne peut donc être liée à la pêche. Ce déclin, combiné à l'accroissement de la mortalité naturelle entre les stades d'œuf et de juvénile pélagique d'une année à l'autre, est conforme aux mécanismes anticompensatoires notés chez des populations de poissons.

Introduction

A commercial fishing moratorium was implemented for the northern cod stock (NAFO Div. 2J3KL) in July 1992, following a severe decline in abundance (Taggart et al. 1994). In the absence of fishing, a population is expected to increase in abundance. Myers et al. (1997) predicted that the northern cod stock would double in size approximately every four years, based on an intrinsic rate of natural increase estimated by fitting a Ricker curve to the historical data for this stock. Similarly, Roughgarden and Smith (1997) predicted there should over 1.5 million tonnes for the northern cod stock by 1998. Traditional stock assessment methods estimated that the population for cod, age three and older, was 58 million fish in January 1992 (Murphy et al. 1997). This population was dominated by four and five year old cod from the 1986 and 1987 year-classes and represented < 27,000 t of spawning biomass. Independent estimates from acoustic surveys indicate significantly greater spawning biomass in the spring of 1992 (Rose et al. in press). However, even taking the lower biomass estimates, this population should have increased to > 100 million fish and a spawning biomass in excess of 50,000 t by 1996, based on the prediction of Myers et al. (1997). However, the most recent stock assessment indicated that by 1998 the spawning stock biomass has not increased at this rate (Lilly et al. 1998).

Accurately assessing the production of the northern cod stock requires new measures that target key stages of their life history. Traditional stock assessment methods for the northern cod have largely become ineffectual following the collapse of the population. In the absence of a directed commercial fishery since 1992, catch, effort and age data are no longer available as input into the traditional sequential population models (SPA). Trawl surveys have been carried out by the Department of Fisheries and Oceans in the late autumn, assuming adult cod had migrated to overwintering areas on the shelf where they would spawn the following spring. Recently, these surveys have not located adult concentrations offshore (Lilly et al. 1999), indicating that a seasonal migration no longer occurs (Rose 1996). The inshore areas of Newfoundland and Labrador are not systematically surveyed for stock assessment purposes, yet recent studies have demonstrated this is the primary nursery area for juvenile cod (Dalley and Anderson 1997, Anderson and Gregory 2000).

Recently, two new research programs were initiated to measure stock performance during the rebuilding period of the northern cod population. An acoustic survey designed to measure the abundance of adult and demersal juvenile cod of the northern cod stock off southern Labrador during the spring post-spawning period began in June 1994. The survey centered on Hawke Channel (Figure 1), which approximates the historical northern spawning area of this stock (Templeman 1981, Hutchings et al. 1994). It has been hypothesized that successful recruitment in northern cod is dependent on significant spawning occurring in this northern area, as a consequence of high probability for retention of eggs and larvae over the shelf (deYoung and Rose 1993). Second, a juvenile fish pelagic trawl survey began in August of 1994, to measure the distribution and abundance of pelagic juvenile cod throughout the entire coastal and shelf regions of Newfoundland and Labrador following spring spawning (Figure 1, Anderson and Dalley

1997a). Historically, pelagic juvenile cod were abundant on the shelf following the period of egg and larval drift (Anderson et al. 1995). Measuring the distribution and abundance of pelagic juvenile cod is designed to give an early measure of recruitment that will relate to the broad scale spawning distribution of northern cod. It is also an important measure of production by the stock, before settlement and the pre-recruit period of survival when inter-specific and intra-specific predation may significantly alter year-class abundance.

The purpose of this paper is to report on the initial findings of these two surveys, 1994-1996, and compare observations of offshore spawning in spring with the production of pelagic juvenile cod each year. We report the abundance of post-spawning cod in the Hawke Channel area in spring and that of pelagic juveniles each following summer for all coastal and shelf areas of the northern cod. We estimate the total number of eggs produced based on the abundance, maturity and fecundity of observed spawners and compare the magnitude of our independent estimates of eggs and pelagic juveniles each year.

Materials and Methods

Demersal Cod

An acoustic survey was conducted in the Hawke Channel area in NAFO Division 2J in June of 1994 to 1996 (Figure 1). A randomly started grid of transects was run over the area with the goal of attaining widespread coverage of the area from approximately 200 to 700 m, which brackets the area inhabited by cod in this region (Figure 2). The same grid was sampled each year, although sampling effort varied somewhat. A total of 1019, 1580 and 947 km of acoustic transects were run in June of 1994, 1995 and 1996, respectively. Transects were run at 8 knots, in 1994 employing the vessel "Gadus Atlantica", and in 1995 and 1996 the CCGS "Teleost". Both are research trawlers modified specifically for acoustic surveying. Echosounders (38 kHz) were calibrated with tungsten-carbide and copper spheres according to standard procedures (Foote 1987). In 1994 and 1995, a purpose-built dual beam system was deployed from a towed body at approximately 100 m depth. In 1995, seven transects were also run with the new hull mounted EK500 system in the Teleost for comparative purposes. In 1996, the EK500 38 kHz split beam system was used exclusively.

Fishing sets were conducted during each survey to assist signal interpretation and provide biological samples, in particular otoliths for aging, and to record length, weight, and reproductive condition. Sets were targeted at specific "classes" of acoustic signal. All fishing was conducted with the Campelen 1800 research shrimp trawl with small mesh liner. This net is considered an effective sampling tool for cod of 2 y of age and older, although no partial catchabilities are available (Godo and Walsh 1992).

Acoustic data were analyzed initially by displaying all transects graphically to identify individual cod signal (Figure 3). Virtually all cod occurred as groups of targets that were readily recognizable from the acoustic record and unlikely to be confused with other acoustic back-scatter in that region. During these analyses, fishing data and a library of

known acoustic signals were consulted. In virtually all cases, fishing data agreed with independent echogram interpretations. In 1994 and 1995, this process was conducted on older visualization software modified for that purpose. In 1996, the EK500 data was analyzed using FASIT, a new software and analytical program designed for visualizing, separating and quantifying multi-species acoustic signals (LeFeuvre et al., in press). The major task was to separate cod from shrimp, which was highly abundant in the study region. The analytical strategy was to simultaneously threshold the signal at -75 dB (20logR) and edit single targets attributable to cod prior to integration(see Figure 3). We consider these to be minimal absolute estimates, as no additions were made for cod likely to be present within the bottom zone and undetectable by these echosounders (1-2 m). Hence, the estimates should be considered as minimal and relative with respect to true stock size but absolute in the sense that they are converted by known scaling factors to fish densities. Once the species classification and editing of the bottom and any noise was completed, the remaining cod signal was integrated for each 100 m of distance along all transects.

Cod densities were mapped using MapInfo (Figure 2). The contiguous areas of cod were encircled using a mapping tool and the areas of cod aggregations were estimated. To estimate mean backscatter (Sa) and confidence intervals, a bootstrap method was employed. Acoustic transect data within the aggregations were 25 times re-sampled at a rate of 2%, to reduce autocorrelation in the density data. The 25 means were then used to estimate the 95 % confidence intervals, defined as the 2.5 and 97.5 percentiles of the frequency distribution of boostrapped means.

Mean Sa values were absolute densities using a target strength to length model of TS (dB) = 20 Log L (cm) - 67.5 (modified from Rose and Porter 1996, Foote 1987) and detectabilities determined experimentally (Lawson and Rose 1999). Each 4 cm length group was scaled separately as a component of the overall Sa, based on the proportion of each length group in the overall catch. Note that variance includes sample error and an uncertainty in the assigned target strength of 1 dB. An age to length key based on otolith sampling conducted during this research was used to convert length to age to estimate abundance at age. A weight to length conversion based on a model developed for the biological samples was used to estimate biomass.

All cod were fully sampled in 1995 and 1996. In 1994, a random sample of fish caught was fully sampled, and the remainder were measured for length only. Biological measurements included gender, length (cm) and whole, gutted and organ weights (g). Otoliths were taken and read from all fully sampled fish for ageing. Female gonad condition was categorized as either immature or mature, with mature gonads further divided into three stage, according to Morrison (1990). Ripening females had visible opaque eggs. Spawning females had gonads with hydrated eggs, and possibly some eggs already extruded. Spent females had completed spawning, and had no or very few hydrated eggs. Males were judged to be either immature, ripening (testes enlarged but no visible milt), partially spent (testes enlarged with visible milt), or spent. An estimate of the number of eggs spawned each year was based on the acoustic estimates of abundance

in relation to maturity and fecundity at each age, where we assumed a male:female ratio of 50%. Fecundity was estimated from the age--fecundity relationship of May (1967).

Pelagic Juvenile Cod

Pelagic juvenile fish surveys were carried out in August and September each year, with the mid-date occurring approximately two weeks later in 1995 (Table 1). The survey design is based on a systematic survey grid at 55 km (30 nm) station spacing. This design is equivalent to a systematic stratified sampling design, where the first station was selected randomly from one 55 x 55 km stratum (Snedcor and Cochrane 1967). Within the bays, stations were positioned approximately 55 km apart. The surveys were carried out as a multi-species trawl survey of the plankton and nekton of the northwest Atlantic, as described in Anderson and Dalley (1997b).

Pelagic juvenile cod were captured by a mid-water trawl, IYGPT (International Young Gadoids Pelagic Trawl). This is a standard trawl designed to catch pelagic juvenile gadoids with an effective opening averaging 7.9 high by 9.3 m wide (Anderson and Dalley 1997a). The IYGPT trawl was towed at 1.25-1.5 m s^{-1} for 30 minutes, slowly oscillating the head rope between 20-50 m depth through two complete cycles sampling the 20-60 m depth stratum. The trawl depth and configuration were monitored using acoustic net sensors (Scanmar) to measure net depth, net opening, wing and door widths. These data were used to estimate the volume of water (m^3) filtered during the tow to standardize catch rates. The IYGPT catches were processed at sea, identifying all fish to species level, where possible, and recording total length for dominant fish species. Sorted samples of Atlantic cod (*Gadus morhua*) were preserved in alcohol (1994) or frozen (1995, 1996).

Absolute abundance of pelagic juvenile cod offshore (Figure 1) was based on the standardized catch rates at each station, as

$$N_1 = \sum_{i=1}^{k} q \cdot A \cdot C_i \cdot D_i$$

where N_1 is the absolute number of cod offshore, q is the trawl catchability, A is the area represented by each station (2.92 x 10^9 m^2), C_i is the density of cod estimated at each station (m^{-3}), D_i is the maximum tow depth (m), and i represents the number of stations sampled offshore. For all inshore areas (Figure 1), absolute abundance was estimated, as

$$N_2 = \sum_{j=1}^{m} q \cdot B_j \cdot \sum_{i=1}^{k} E_i \cdot D_i$$

where N_2 is the absolute abundance inshore, q is the trawl catchability, B_j is the total area of each inshore area (m^2), E_i is the mean density of cod for all stations sampled within each inshore area (m^{-3}), D_i is the mean maximum tow depth (m), i represents the number of stations within each inshore area, and j represents the inshore areas. The inshore areas

were estimated using a high resolution shoreline to define the inner boundary, while the outer boundary was defined arbitrarily to include an outer extension of each bay onto the adjacent shelf. Area was estimated using Surfer (1997). Total abundance for the entire stock area, 2J3KL, was simply N_1+N_2. Trawl catchability was estimated for an IYGPT by Koslow et al. (1997), where ($q = 0.14$). Catchability for nekton typically ranges from 0.1 to 0.25 (Sundby et al. 1989, Koslow et al. 1997).

Results

Spawning Cod

The abundance of cod surveyed in Hawke Channel increased from 20 million fish in 1994 to 21 million in 1995 then decreased to 16 million fish in 1996 (Table 2). Total biomass decreased from 17,500 t in 1994 to 8,200 t in 1995 and 5,500 t in 1996, while spawning biomass decreased from 11,700 t, to 2,000 t and finally 900 t, respectively. The increasing abundance contrasted with a decreasing biomass resulted from the disappearance of older fish in the survey area, concomitant with an increase in juvenile cod (Figure 4). Cod age five and older represented 75% of all fish surveyed in 1994 and 89% of the biomass. However, in 1995 and 1996 cod age five and older only represented 14-13% of all fish surveyed and 31-34% of the biomass. These older cod represented the mature fish, where cod age five ranged from 28-61% mature each year.

During the three survey years in Hawke Channel, we measured an increase in the abundance of the 1990-93 year-classes at ages 2-5 years (Table 3). This increase was probably not due to trawl catchability, as increasing abundance occurred for cod ages and lengths considered to be fully recruited to the Campelen trawl (Godo and Walsh 1992). In addition, the 1992 year-class did not occur in the 1994 survey at age two but two year old cod occurred abundantly in both the 1995 and 1996 surveys. In contrast, there was a significant decline in the abundance of older cod, ages 5-7 years, from the 1987-89 year-classes (Table 3). The declines in abundance of the older, mature cod were quite severe. For example, the 1987 and 1988 year-classes disappeared entirely from the survey areas in 1995 as age seven and eight year old fish. In other cases, declines in abundance ranged from a decrease of 33% from age 4-5 for the 1992 year-class to 79-93% for cod aged 4-8 years for the 1988-91 year-classes. Overall, the observations among surveys suggests an invasion of age two to four year old juvenile cod into the Hawke Channel survey area in 1995 and 1996. The disappearance of older cod exceeded any reasonable estimates of natural mortality.

The reproductive condition of cod declined significantly among years (χ^2, $P < 0.05$). In 1994, approximately 55% of the cod were mature, declining to 25% in 1995 and 15% in 1996. In all cases, the ratio of mature females was greater than mature males. In all three years, only an occasional spawning fish was encountered (< 1%) and most fish were judged to be recently spent, indicating that spawning was complete by the time of the survey each year. Cod matured at very young ages in Hawke Channel, attaining > 50% maturity at less than five years of age (Figure 5). This was similar to, but slightly younger

than, the proportion mature estimated in annual autumn research vessel surveys (Figure 5).

We estimated that the total numbers of eggs produced each year by cod spawning in Hawke Channel declined from 3.7×10^{12} in 1994, to 6.5×10^{11} in 1995 and 2.7×10^{11} in 1996 (Table 2).

Pelagic Juvenile Cod

The abundance of pelagic juvenile cod decreased significantly from 3.1×10^{9} in 1994, to 1.5×10^{9} in 1995 to 1.8×10^{8} in 1996, a decrease in abundance that exceeded an order of magnitude (Figure 6). The decline in abundance first occurred offshore in 1995, decreasing by a factor of six compared to 1994. Inshore, abundance remained relatively high in 1995, comparable to that of 1994. By 1996, offshore abundance declined by over two orders of magnitude compared to 1994 and over an order of magnitude compared to 1995. Inshore in 1996, abundance decreased by a factor of approximately 7.4 compared to 1994 and 1995.

Pelagic juvenile cod occurred throughout the inshore area in 1994 and they were also distributed widely offshore over the Northeast Newfoundland Shelf, although only a few cod occurred on the southern portion of the Northeast Newfoundland Shelf and on the northern Grand Bank (Figure 7). In 1995, juvenile cod only occurred sporadically offshore over the Northeast Newfoundland Shelf, although they remained widely distributed throughout the inshore. In 1996, only a very small number of pelagic juvenile cod were found at three stations in Bonavista Bay, one station in White Bay and at one station off the northern peninsula. None occurred in Notre Dame Bay, Trinity Bay or Conception Bay and juvenile cod were only observed at one station offshore.

Pelagic juvenile cod were approximately the same size each year. Cod averaged 45.1 mm (30-101 mm), 45.3 mm (27-71 mm) and 41.2 mm (26-62 mm) total length in 1994-1996, respectively. Based on micro-otolith analysis, these cod ranged in age from an average of 81 days of age in 1994 to 69 days in 1995 and 64 days in 1996.

There was very little difference in the size and age of pelagic juvenile cod between inshore and offshore areas. For example, in 1994 when cod were distributed widely over the shelf, the length offshore was 45.0 mm compared to 44.8 mm inshore. Converting age frequency distributions to larval hatching dates demonstrated that cod spawning occurred primarily in May of 1994, whereas it occurred throughout May and June of 1995 and 1996 (Anderson and Dalley 2000). A comparison of the hatching dates between inshore and offshore areas in 1994 demonstrated that hatching started 14 days earlier inshore but in both areas hatching was complete by the end of June (Figure 8). The mean hatching date was only five days later in the offshore.

Mortality Estimates

Declines in abundance of eggs spawned each year and the abundance of pelagic juvenile cod found offshore on the Northeast Newfoundland Shelf were in proportion, declining by over an order of magnitude among years in each case (Figure 9). We can estimate natural mortality each year from eggs to pelagic juveniles, based on our independent estimates of abundance, as $z = \frac{(\ln(N_1) - \ln(N_0))}{t}$, where N_0 is the abundance of eggs spawned in Hawke Channel and N_1 is the abundance of pelagic juveniles sampled offshore. Time, t, was the difference between mean spawning times estimated by Anderson and Dalley (1999) and the mean date of capture for pelagic juveniles. Based on this calculation, natural mortality was estimated to be -0.068 d^{-1} in 1994, -0.084 d^{-1} in 1995 and -0.112 d^{-1} in 1996. These mortalities compare to a modelled estimate of -0.081 d^{-1}, based on median parameter values for the egg-juvenile period, and a range from -0.050 d^{-1} to -0.111 d^{-1} for extreme parameter values (Anderson et al. 1995).

Discussion

There are expectations that a fish population will increase in abundance under a complete fishing moratorium. Predictions of rapid increases in population size by Myers et al. (1997) and Roughgarden and Smith (1997) are based on historical data.
However, there are several values of population growth rate (r) for a species, depending on the age composition, specific growth rates and age specific maturity (Odum 1971). It is naive to use historical data to predict the intrinsic rate of increase for a collapsed population that may be less than 1% of its historical mean size and no longer exhibits normal behaviour, such as seasonal migrations between inshore and offshore areas.
Our observations are indicative of depensatory mechanisms in the remaining offshore spawners of the northern cod population. The form of this depensation appears to be primarily in the loss of the spawning fish, declining at rates that exceed any 'normal' level of natural mortality. The high loss rates of fish from Hawke Channel is consistent with fish not returning to this area to spawn in 1995 and 1996.

The acoustic survey was restricted to the Hawke Channel spawning area, historically believed to be the most important offshore spawning area (Templeman 1981, Hutchings et al. 1994). However, the pelagic juvenile fish survey covered the entire shelf and coastal areas each year. The close agreement between the survey results indicates that the only remaining spawners offshore occurred in the north of the northern cod stock area (2J3KL), and that these spawners had largely disappeared by 1996. It is noteworthy that the abundance of adult cod caught in the autumn offshore trawl survey actually increased 1994-1996 (Lilly et al. 1999). Spawning cod also occurred inshore during these years (Smedbol et al. 1998). The continued broad distribution and relatively high abundance of pelagic juvenile cod inshore in 1995, compared to few offshore, supports the notion that spawning by inshore cod was widespread in both 1994 and 1995. Smedbol et al. (1998) estimated that 1.83×10^{12} eggs were produced by 16,800 t (Rose 1996) of spawning cod in Smith Sound, Trinity Bay in the spring of 1995.

We estimated that natural mortality increased each year, where this mortality would operate primarily on the egg and larval stages. Mortality estimated in 1994 and 1995 was relatively low to mid-range while mortality in 1996 reached near maximum values, compared to modelled estimates (Anderson et al. 1995). A multi-species survey of the entire pelagic fish community demonstrated that abundance decreased for all species, 1994 to 1996/97 (Dalley et al. 2000). These species included redfish (*Sebastes*} sp.), Arctic cod (*Boreogadus saida*), sandlance (*Ammodytes* sp.) and American plaice (*Hippoglossoides platessoides*). All species were pelagic young-of-the-year planktivores, with the exception of sandlance that also included older age groups but, nevertheless, are still planktivores. This common decline in 0-group abundance across such disparate species lines suggests poor survival conditions occurred during the 1994-1996 period.

Given the low level of spawning cod in the 2J3KL area and the high mortality rate estimated in 1996, this may be another form of depensation, where spawner abundance is so low that high early life history mortality can effectively eliminate a year-class. The relative ranking of year-classes measured here, as 1994 > 1995 > 1996, is the same as that estimated at ages one and two years old in the demersal autumn trawl survey (Lilly et al. 1999). In fact, the 1996 year-class estimate is the lowest ever recorded for this stock. Simple measures of spawning stock biomass, traditionally used to estimate stock size, can be an unreliable estimate of the number of viable eggs produced each year (Marshall et al. 1998, Marteinsdottir and Thorarinsson 1998). Combining estimates of spawning fish in spring with the abundance of pelagic juvenile cod measured before they settle to the bottom can provide the two most important measures of stock performance in the absence of fishing. Together, these estimates can provide a true measure of the intrinsic rate of natural increase in fish.

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Table 1. Summary of pelagic juvenile fish surveys conducted 1994-1996. IYGPT – International Young Gadoids Pelagic Trawl. DoY – Middle survey day of the calendar year.

Year	Survey dates	DoY	IYGPT stations
1994	22 Aug – 3 Sep	234	99
1995	5 Sep – 22 Sep	248	139
1996	19 Aug – 6 Sep	231	147

Table 2. Abundance, biomass (t) and egg production of Atlantic cod surveyed offshore in the spring of 1994-1996. Total eggs were estimated from abundance, maturity and fecundity parameters for each age. Values in parentheses represent the 95% confidence intervals estimated from the acoustic survey data (see text for details).

Year	Abundance	Total biomass (t)	Spawning biomass (t)	Total eggs
1994	20.2×10^6	17,500	11,700	3.7×10^{12}
	(16.9 – 23.1)	(14,700 – 20,000)	(9,900 – 13,400)	(3.1 – 4.2)
1995	20.9×10^6	8,200	2,000	6.5×10^{11}
	(16.4 – 24.9)	(6,500 – 9,800)	(1,600 – 2,400)	(5.1 – 7.7)
1996	15.5×10^6	5,500	900	2.7×10^{11}
	(11.5 – 20.0)	(4,000 – 7,000)	(700 – 1,100)	(2.0 – 3.5)

Table 3. Year-class abundance (x 10^6) surveyed in Hawke Channel, 1994-1996, for Atlantic cod (*Gadus morhua*) age two years and older. The numbers in parentheses are the ages of cod, where the youngest cod captured were age two.

	Survey		
Year-Class	1994	1995	1996
1986	0.20 (8)	0.0 (9)	0.0 (10)
1987	1.96 (7)	0.0 (8)	0.0 (9)
1988	4.38 (6)	0.0 (7)	0.0 (8)
1989	8.53 (5)	0.63 (6)	0.05 (7)
1990	2.68 (4)	2.29 (5)	0.33 (6)
1991	2.42 (3)	8.00 (4)	1.69 (5)
1992	0.0 (2)	6.81 (3)	4.60 (4)
1993		3.15 (2)	5.22 (3)
1994			3.61 (2)

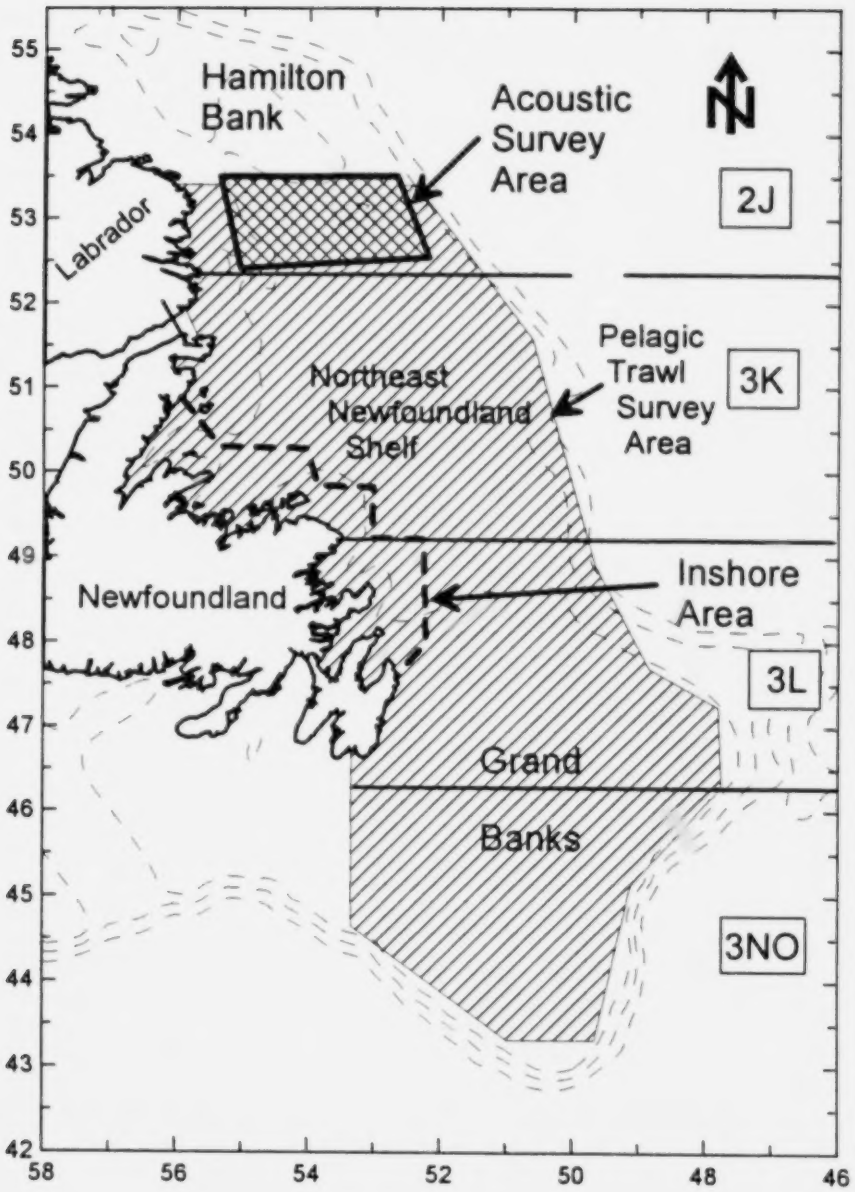

Figure 1. The northwest Atlantic shelf areas off Newfoundland and Labrador. The shaded area represents the geographical extent of the pelagic juvenlie fish surveys, while the polygon (white) outlines the spring acoustic survey area in Hawke Channel. The inshore and offshore areas along the northeast coast of Newfoundland is demarcated by the dashed line. The isobath lines span depths from 200, 500 and 1,000 m.

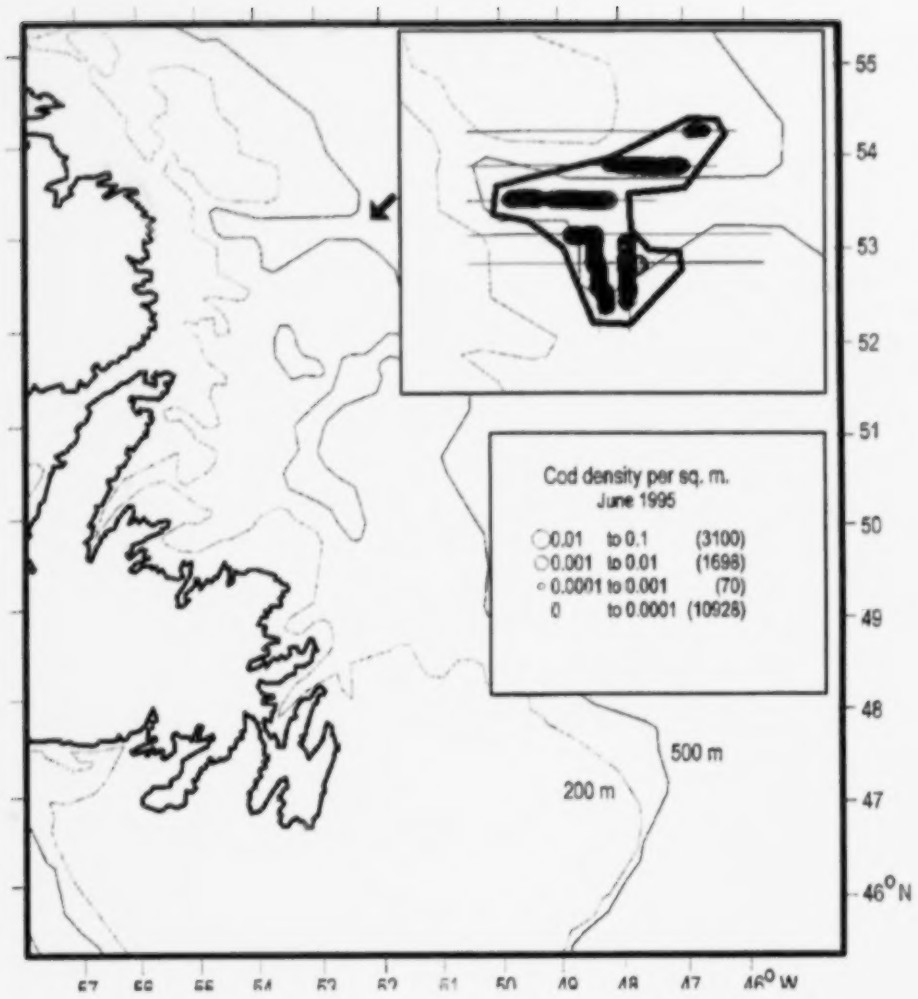

Figure 2. Acoustic survey tracks sampled in Hawke Channel each spring, showing the distribution of acoustic cod distribution in 1994.

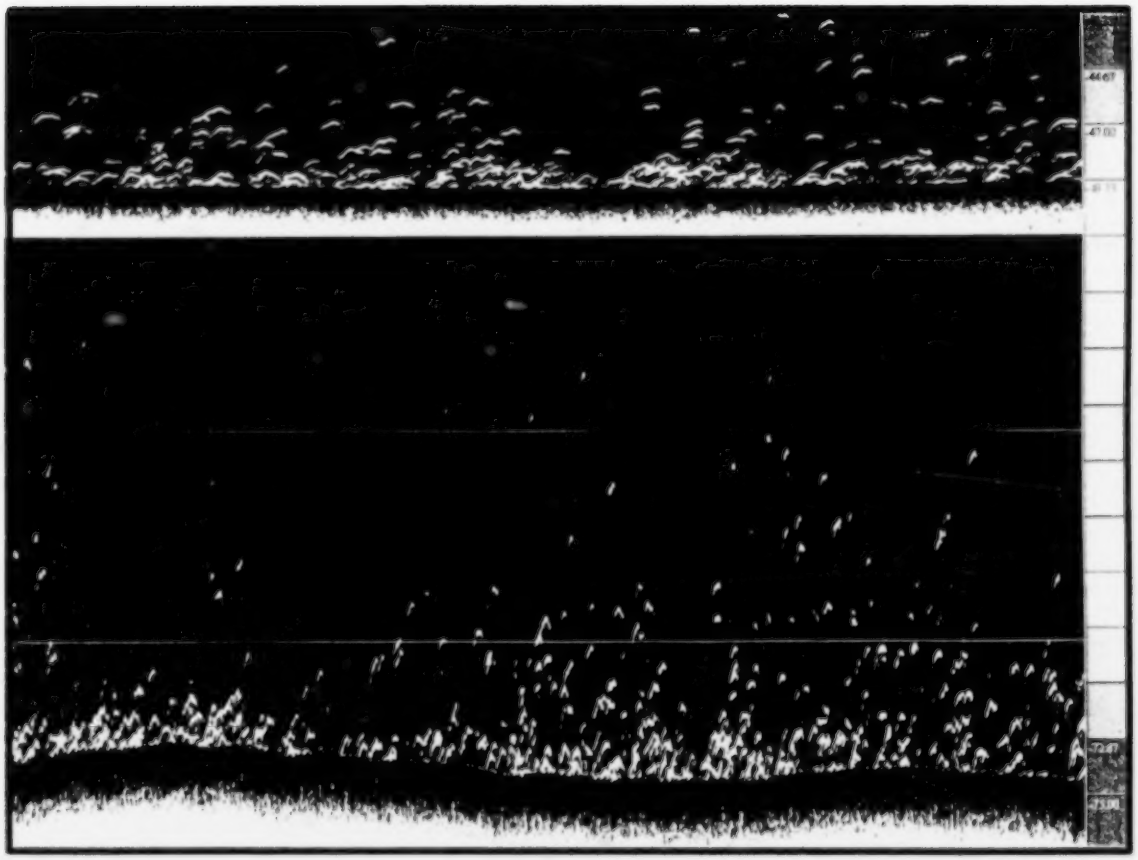

Figure 3. Acoustic image of post-spawning cod in Hawke Channel, June 1996 at approximately 400 m depth. The full echogram spans approximately 7 km. The expansion window is a portion of the 7 km total to show details of fish distribution near the bottom.

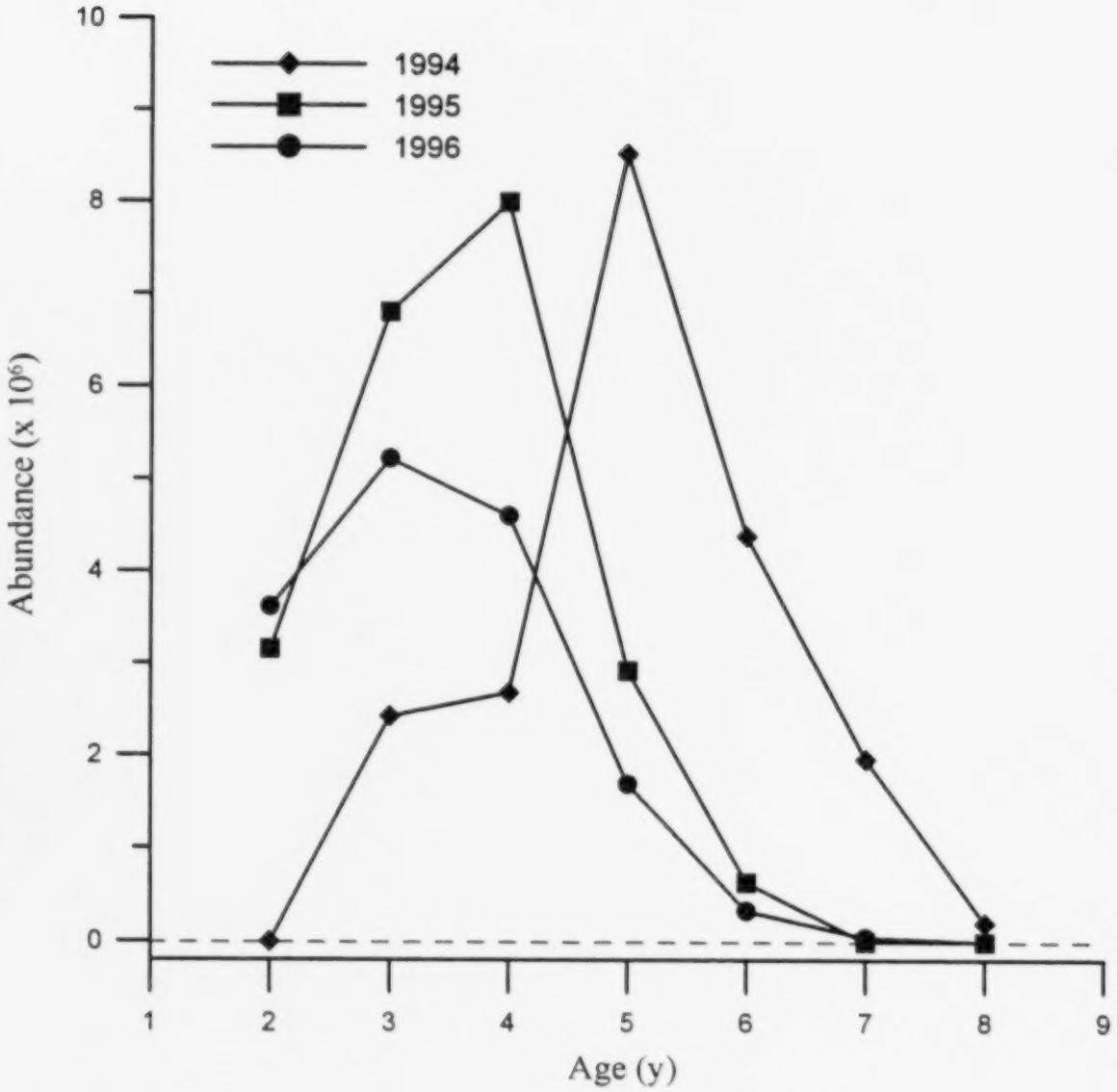

Figure 4. Abundance of cod estimated for each age group in acoustic surveys 1994-1996 in the Hawke Channel.

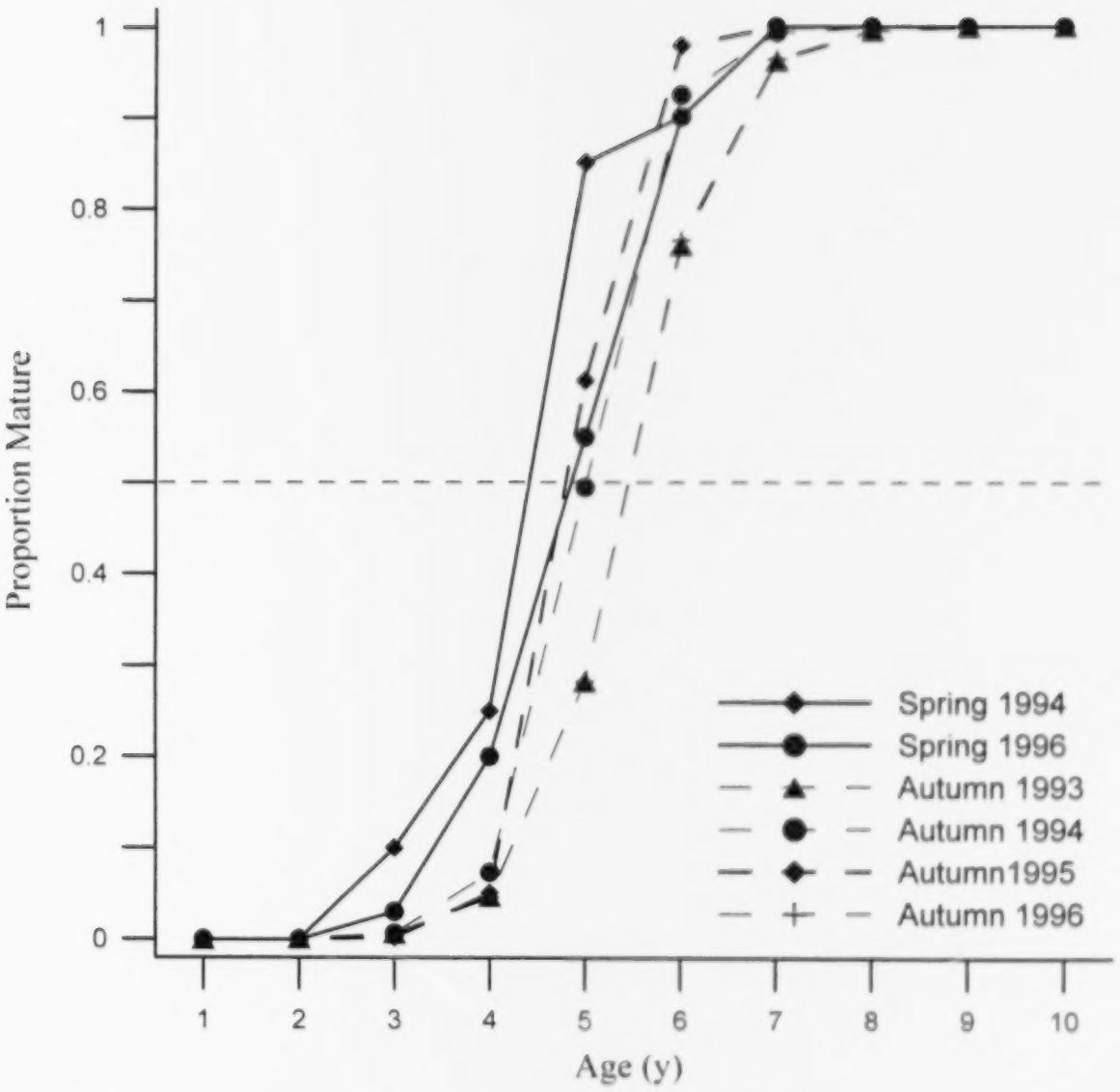

Figure 5. Proportion of cod mature sampled in Hawke Channel during June of 1994-1996 and during autumn research vessel surveys 1993-1996. The dashed line represents 50% mature.

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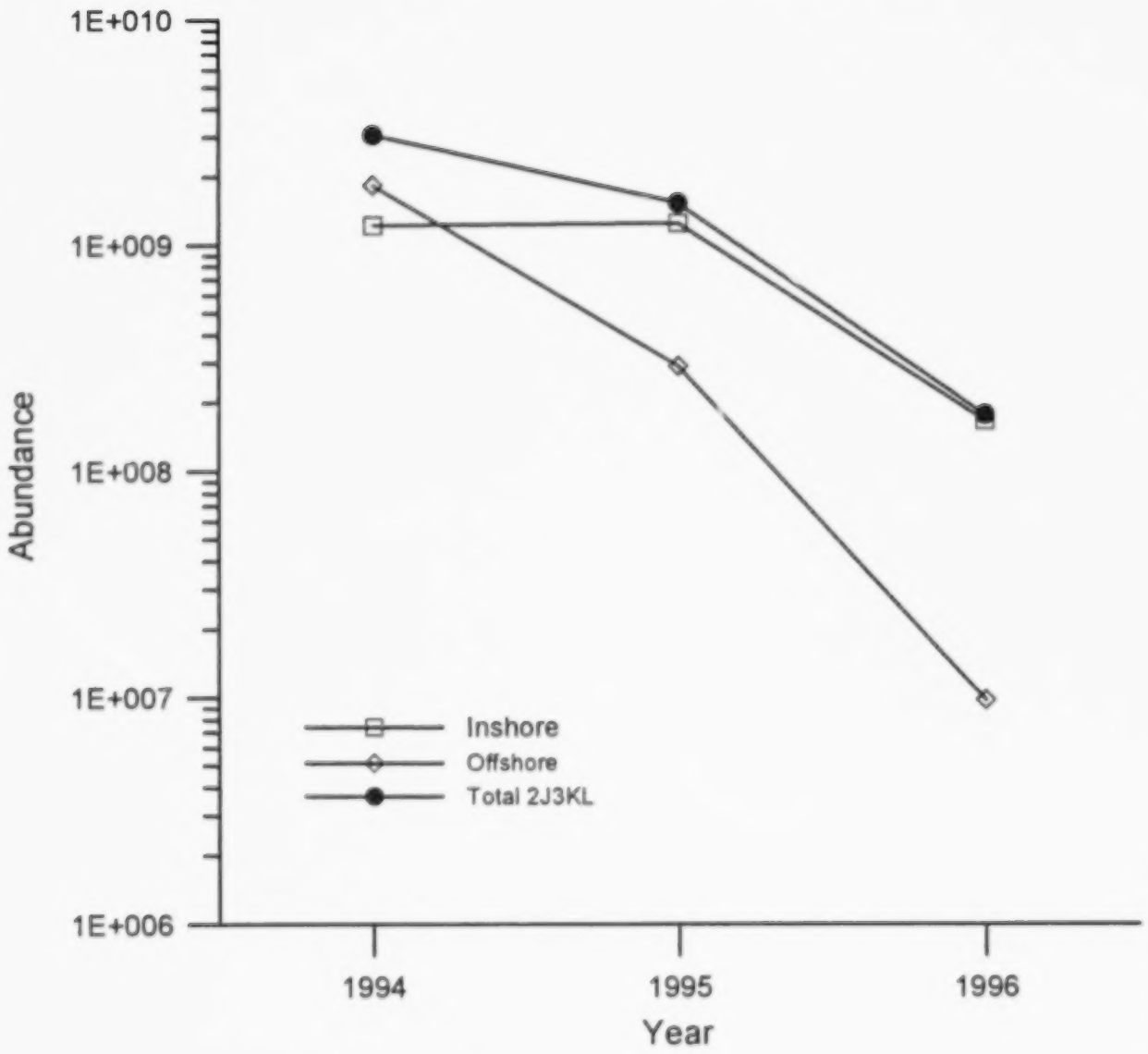

Figure 6. Absolute abundance estimates of Atlantic cod based on pelagic juvenile fish surveys, 1994-1996.

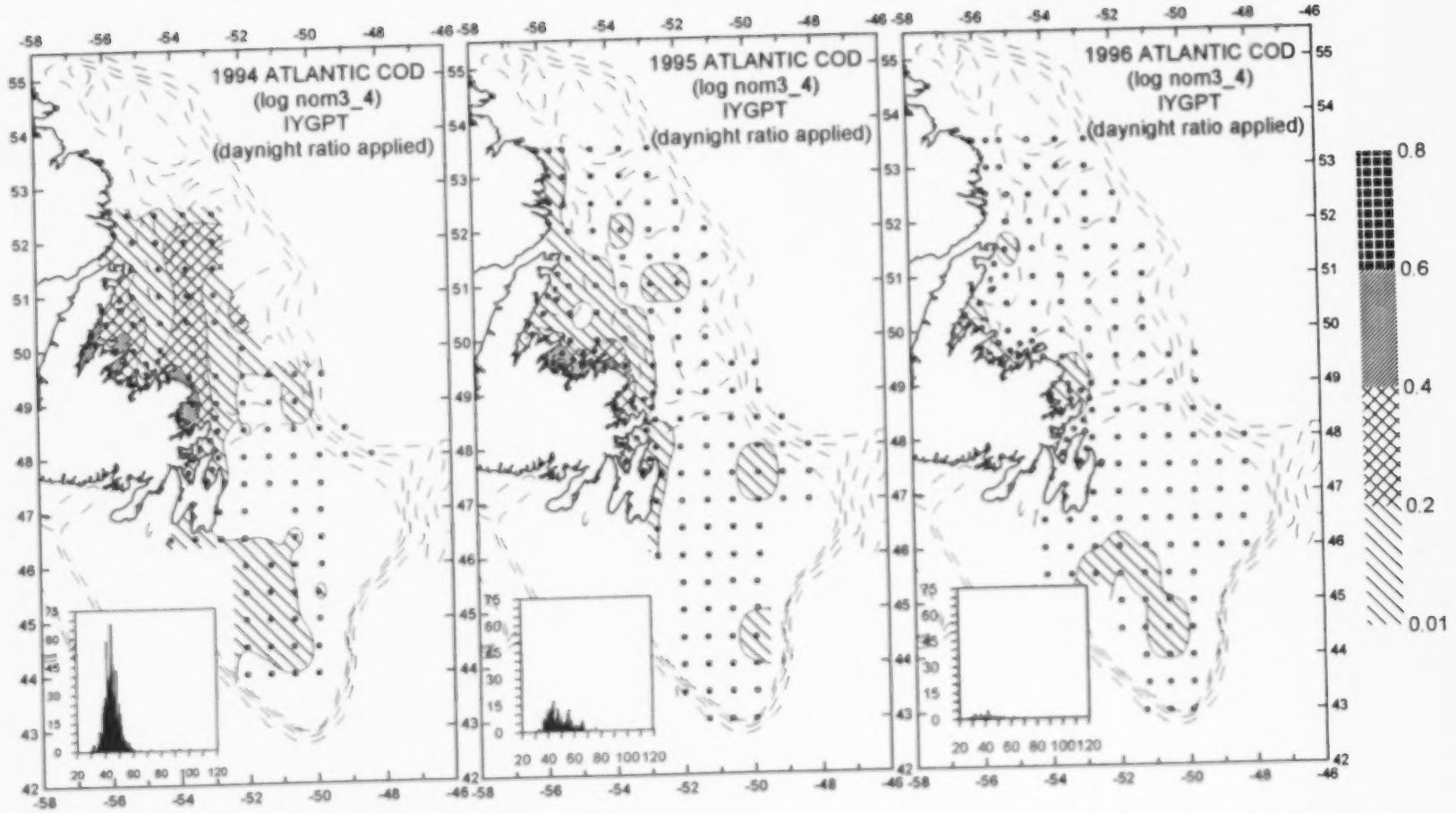

Figure 7. Distribution of pelagic juvenile cod sampled with the IYPGPT trawl August-September 1994-1996. The dots represent sampling stations and the blank shading areas where no cod were caught. The contours are linear intervals of log-transformed abundance (number/10,000m^3).

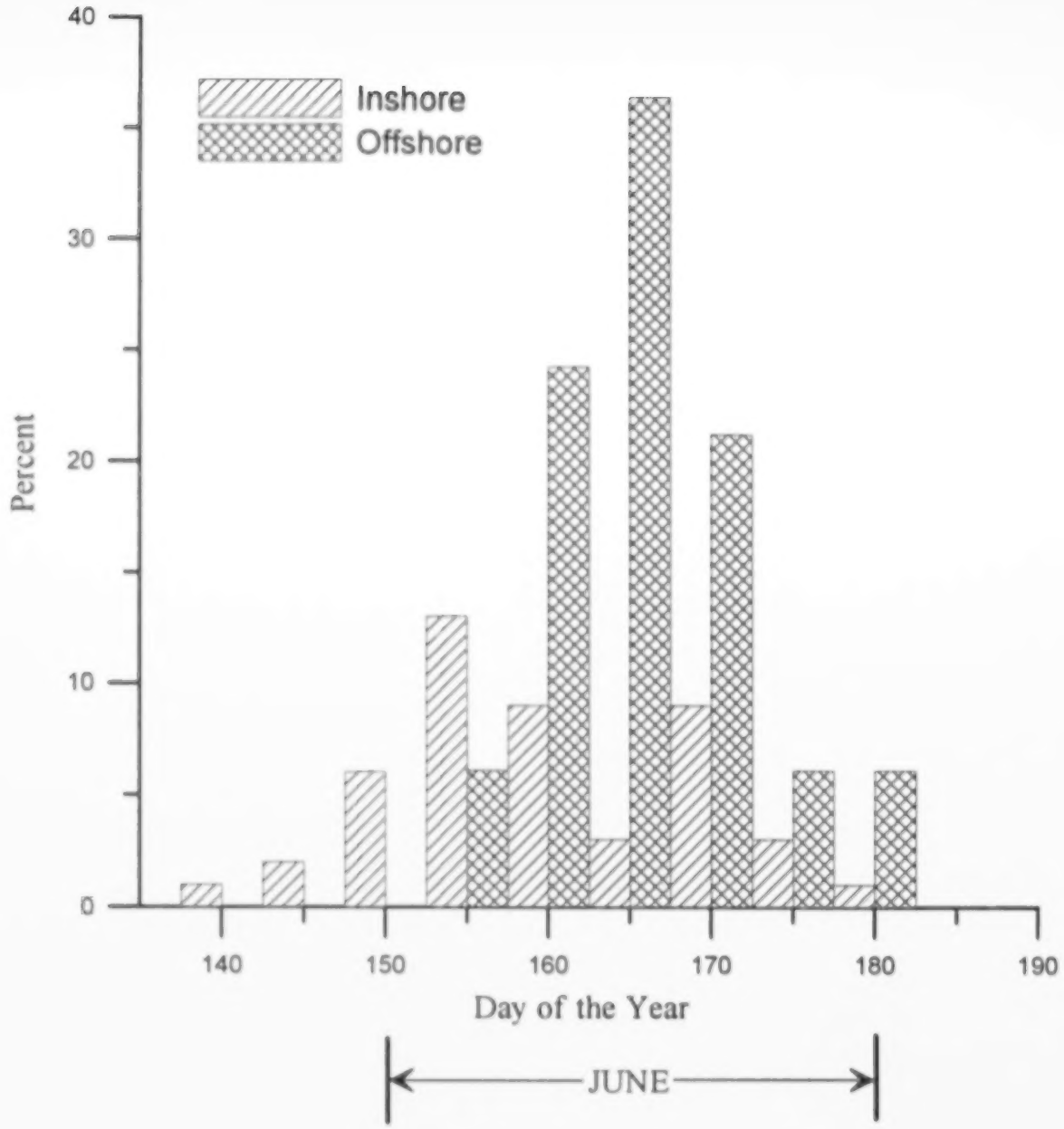

Figure 8. Hatching day frequency distributions for pelagic juvenile cod sampled inshore and offshore in 1994.

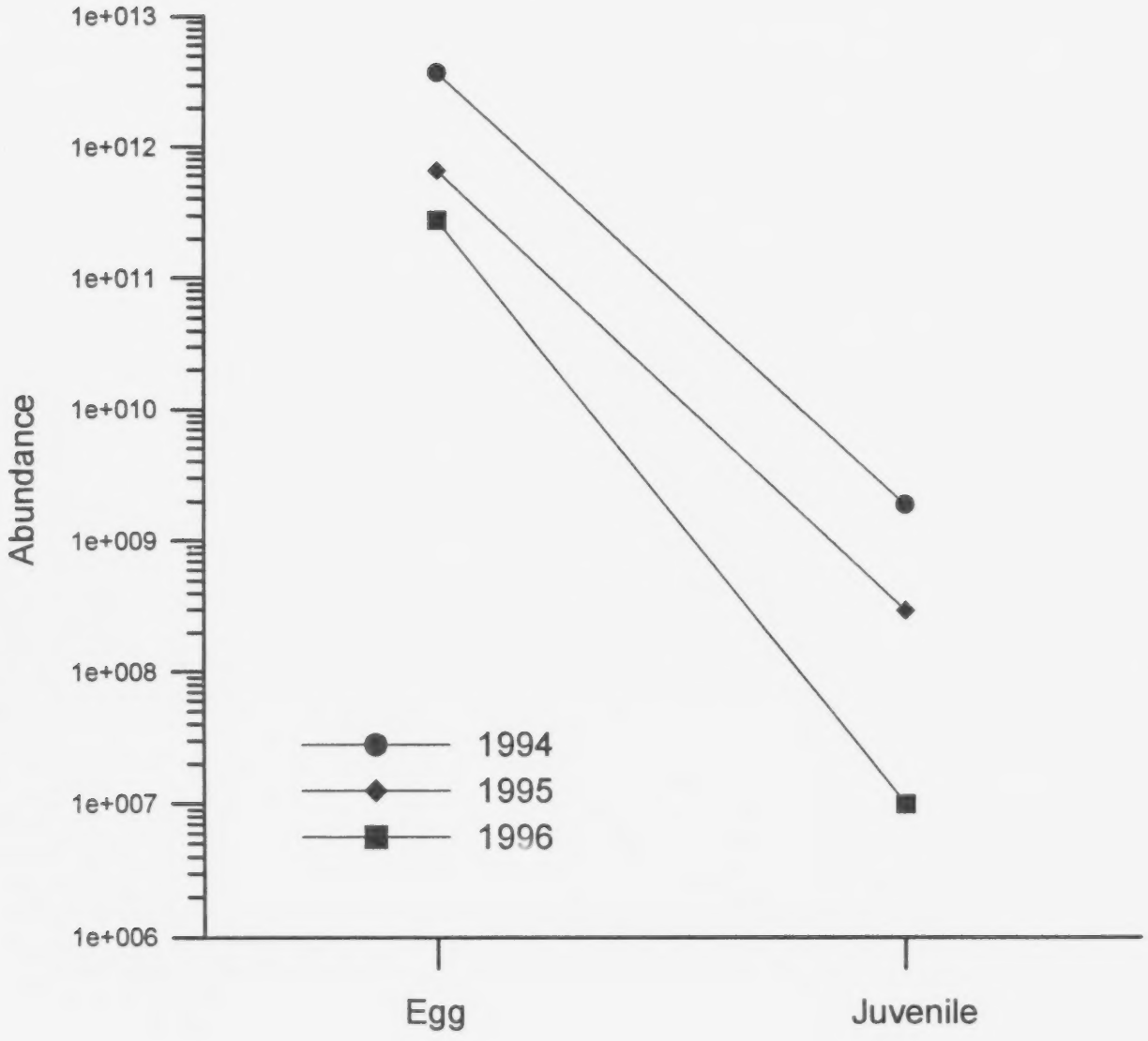

Figure 9. Abundance of eggs produced each year in Hawke Channel estimated from spring acoustic surveys and the corresponding abundance of pelagic juveniles sampled offshore estimated from the pelagic fish trawl surveys.